

*QUANTENOBDELLA HOWENSIS* RICHARDSON 1969 OF LORD HOWE ISLAND, WITH COMMENT ON DISPERSAL BY PASSIVE TRANSPORT (HIRUDINOIDEA: RICHARDSONIANIDAE)<sup>1</sup>

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**Abstract**

Distinct in having 16 5-annulate somites, salivary gland papillae, elongate cylindrical ejaculatory bulbs and a simple fusiform vagina with a long vaginal duct. Adequate systematization gives evidence of diversity in leech faunas, not the widespread uniformity associated with dispersal by passive transport.

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**Introduction**

The elongate cylindrical ejaculatory bulb folding lengthwise in contraction and in male maturity, had not been recognized as a distinctive morphological form at the time when the original description of the g. *Quantenobdella* was prepared (Richardson 1969a), and at that time I failed to detect the minute salivary gland papillae reported here on the jaws.

With the combination of these papillae and 16 complete 5-annulate somites, elongate cylindrical ejaculatory bulbs as in bassianobdellids (Richardson 1970a) and a simple fusiform vagina, poorly defined internal muscular ridges on the wall of the pharynx, *Quantenobdella* now stands apart from the other genera of aquatic jawed sanguivores known in the Australian Region, but otherwise the morphology retains it fully within the Richardsonianidae.

The inadequately known *Hirudo catenulata* Johansson 1918 of the New Hebrides resembles *Q. howensis* in having 16 complete 5-annulate somites, a small posterior sucker about half of the maximum width of the body, and a small number of teeth, but differs in pattern, and Johansson states that there are no salivary gland papillae (which may or may not be correct for his specimens were small, 20.0 mm in length).

The presence of salivary gland papillae on the jaws is known in aquatic jawed sanguivores of the tropical-subtropical belt, essentially between the latitudes of 35° N. and S. Others

lacking such papillae occur in this belt and in the temperate regions. The present indications are (1) that *Quantenobdella* is part of the tropical-subtropical component in the Australian leech fauna, and (2) in favour of the probability of isolation over a period of biological time sufficient for the appearance of distinctive generic characteristics.

The occurrence of leeches on oceanic islands has been long known. Moquin-Tandon (1846) records leeches in the East Indies and the West Indies. By 1900 Blanchard (e.g. 1897) had reduced many early described species in the East Indies to a relatively few species widely distributed through the archipelago. Since 1900 leeches have been recorded on many remote high oceanic islands: Madagascar, Juan Fernandez, Samoa, Hawaii, Fiji, etc. The knowledge of these more isolated leech faunas is commonly incomplete, inadequate (even for Hawaii), and confused within the earlier simple classification based essentially on readily accessible external morphological features with the recognition of relatively few genera, some being widespread, and a small number of species.

These leeches are without close marine relationship, are intolerant of saltwater, and are freshwater dependent. The distribution of a few genera throughout an archipelago and the appearance of a uniformity in the fauna, are suggestive of the possibility of passive transport by other animals or through the agency of man, as proposed by Darwin as a dispersal mechan-

ism leading to the uniformity of freshwater faunas over wide areas. The few authors who have concerned themselves with the distribution of leeches on oceanic islands have relied on passive transport as the dispersal mechanism.

For example, Moore (1901) recognized the resemblance in the morphology of the reproductive systems, somital annulation, pattern, etc. of a leech from Porto Rico, the West Indies, to a leech in the Oriental g. *Hirudinaria*, gave the leech from the West Indies the name of *Hirudinaria blanchardi*, and suggested that it had been transported to the West Indies by man. Moquin-Tandon (1846) records shipments of medicinal leeches from Europe to the West Indies, but not from the Oriental Region. Notes associated with later specimens of *blanchardi* now in the Smithsonian Institution, show that Moore continued strongly of his earlier opinion. In 1946, Moore considered that the presence of *Gastrostomobdella quinqueannulata*, *Glossiphonia weberi lata*, and *Barbronia weberi formosana* in Hawaii was probably due to human agency and to transport by birds. Otherwise the g. *Gastrostomobdella* was known in Indo-Malay, *G. weberi lata* in China, and *B. weberi formosana* in Formosa.

The only previous knowledge of the nature of the leech faunas of the high oceanic islands adjacent to the E. coast of Australia is given by Johansson (1918), who described *Glossiphonia novaecaledoniae* and *Barbronia rouxi* from New Caledonia, and *Hirudo catenulata* from the New Hebrides; and by Moore (1944) who described *Chtonobdella parva* from the New Hebrides. This illustrates the nature of the leech faunas of high oceanic islands with representation of glossiphonids, erpobdellids, and aquatic jawed sanguivores, with the addition of terrestrial jawed sanguivores in the Oriental and Australian Regions, including Polynesia.

Passive transport is seemingly possible for jawed sanguivores which attach as adults and young to birds and other animals, but not for long periods, for when engorged, the leech departs the host. The cocoons are deposited loose in wet mud and could conceivably adhere to the feet of birds. This possibility cannot be simply dismissed, but it is questionable that cocoons could be carried for any lengthy time

across the open ocean. Young of the Australian *Aetheobdella hirudoides* perforate the conjunctiva at the outer corner of the eye in some bush birds, including the White-eye, and remain for some weeks in the subcutaneous pocket lateral to the bony orbit (Richardson 1969a). Something possibly of this nature is recorded in Moquin-Tandon for *Hirudo ardeae* at Martinique, but the habit is most rare. The erpobdellids are macrophagous, do not attach to other animals, and fasten the cocoon securely to aquatic plants, sticks, and stones. The glossiphonids take body fluids from aquatic molluscs and other invertebrates, some from amphibia, and brood the young attached to the venter of the adult. Invasion of the nasal chamber of aquatic birds is known for the glossiphonid g. *Theromyzon*.

Prince Edward Island in the Gulf of St. Lawrence has gained a leech fauna since the last glaciation. It was pointed out in a study of the leeches of this island (Richardson 1943) that a possibility of passive transport might be accepted for *Theromyzon* and for the jawed sanguivorous *Macrobdella*, transport of cocoons is a possibility for the macrophagous haemopids, but passive transport was beyond probability for the macrophagous erpobdellids and for the glossiphonids in this fauna. The possibility for passive transport as a mechanism of dispersal is outweighed by the improbabilities. It is necessary to seek a dispersal mechanism which is available to the erpobdellids, the haemopids, and the majority of the glossiphonids. It can be reasonably anticipated that when such a mechanism is found, it will be equally available to *Theromyzon* and *Macrobdella*. The proposal applies also to the leech faunas of high oceanic islands.

More adequate systematization points to dispersal in more remote biological time, a period of such length as has produced diversity at the generic level. Families of regional status, and genera of sub-regional status are now demonstrated for the aquatic jawed sanguivores (Ringuet 1968, Richardson 1969a). It is possible to show (Richardson 1970c) that the Oriental *Barbronia weberi* is not congeneric with *Barbronia rouxi*, the type species of the genus, that *Hirudo catenulata* does not belong

in the g. *Hirudo* (Richardson 1969a), that terrestrial jawed sanguivores of Java, Samoa, and Madagascar placed by Blanchard (1917) in the Australian g. *Philaemon* do not belong in this genus (Richardson 1969b). Also the terrestrial jawed duognathous sanguivore *Nesophilaeon skottsbergi* of Juan Fernandez and the trigonathous g. *Mesobdella* of Chile and the Argentine (Richardson 1970a) belong to the Neotropical jawed sanguivores, not to the Haemadipsidae of the Oriental and Australian Regions. It will be shown later that *Chtonobdella parva* of the New Hebrides differs significantly from the leeches in the Australian g. *Chtonobdella*, that *Hirudinaria blanchardi* differs significantly from the leeches in the Oriental g. *Hirudinaria*, and from a recent study of gastroporous leeches, it is clear that Moore's *quinqueannulata* of Hawaii cannot be retained in the Oriental g. *Gastrostomobdella*.

For aquatic leeches, a measure of uniformity over a wide range is recognizable in those parts of the Western Palearctic and Nearctic which were defaunated in the last glacial and repopulated by a limited immigrant fauna in the postglacial, a period still too brief in biological time for a diversification at specific and generic levels, and division into significant zoogeographic groupings.

In contrast, undisturbed by the last glacial, the aquatic jawed sanguivores of the Australian Region divide at the generic level into provincial faunas. They exhibit not only the diversity of a fauna continuous with the fauna of the long preglacial period, but also the persistence of zoogeographic groupings. Both these features contraindicate dispersal by passive transport.

The progressive displacement of apparent uniformity in distribution by the demonstration of diversity, lowers to improbability the general operation of a dispersal mechanism formerly proposed on the basis of a wide uniformity in distribution.

### Genus *Quantenobdella* Richardson 1969 (Amended)

Monostichodont; 16 5-annulate somites (ix to xxiv); xxv, 4-annulate; somital sense

organs, minute; jaws small, resting in shallow open recesses; teeth, about 40, minute, acute, spaced; salivary gland papillae, sparse, minute; dorsal salivary glands diffuse, with weakly developed columns of aggregated ducts; entrance to pharynx and lumen of pharynx, narrow; weakly defined muscular ridges on the inner surface of the pharynx; pharynx small, terminating in ix; crop compartments in x to xix each with a small pair of simple secondary anterior caeca and larger caeca at the median level, the latter extending into the paramedian chamber and those of xix forming postcaeca extending to xxvi; no copulatory gland pores; genital pores xi and xii  $b_5/b_6$ ; testes, simple saccular; number of testes, ?; anterior region of male paired duct without a primary flexure, epididymis in xii posterior to the elongate cylindroid ejaculatory bulb in xi, the relationship linear; ejaculatory ducts, very short; median reproductive regions, bimyomeric, mesomorphic, both formed on a posteriorly directed primary loop; male median region short, reflected at xi/xii; oviducts, very short; female median region reflected at xiii/xiv; female atrium continuous with the long common oviduct; vagina caecate, transverse, fusiform, vaginal duct long. Size, ? medium, pattern, continuous longitudinal dark bands and light stripes, aquatic, sanguivorous. Australian Region.

Type species: *Quantenobdella howensis* Richardson 1969.

Holotype G850, National Museum of Victoria, 38.0 mm long, from Lord Howe Island, January 1903. W. Baldwin Spencer collector. Right ventrolateral jaw removed, mounted separately.

### *Quantenobdella howensis* Richardson 1969

Fig. 1 a-g

Preserved, moderately contracted so that the annuli are low-ridged, the velum obtuse, the aperture of the anterior sucker transverse, and generally the animal strongly depressed, low convex above, the margins obtusely rounded, the venter slightly concave. Quite typically aquatic, sanguivorous, excepting that the posterior sucker is unusually small. The dorsum divided by narrow light stripes into a median

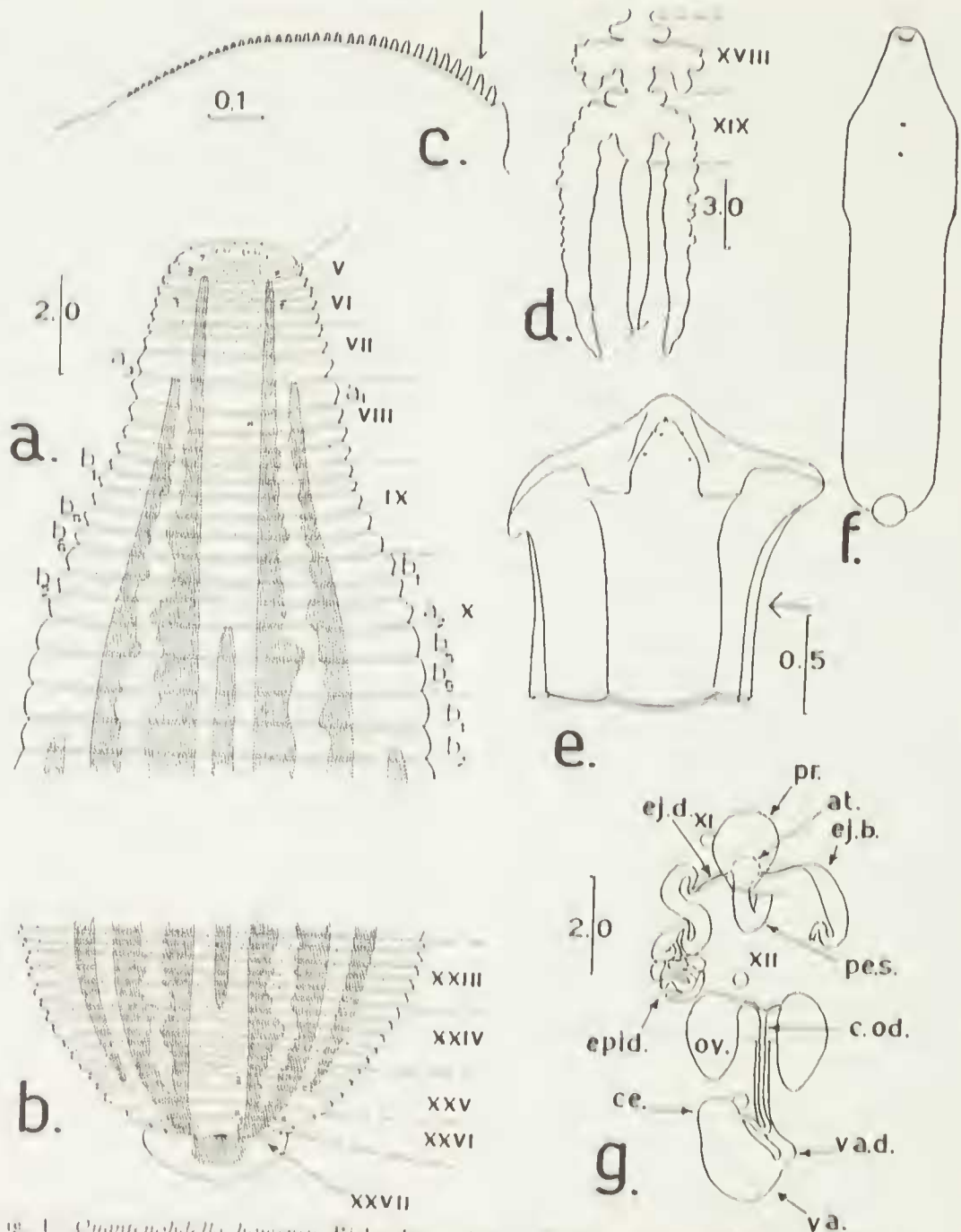


Fig. 1. *Quantenbellula howensis* Richardson 1969: a, Dorsal aspect, somites I to X, and b, somites XXIII to XXVII and sucker, to show annulation and pattern; c, Right ventro-lateral view and dental ridge (arrow marks medial end); d, crop, somites XVIII and XIX, caecation and intestine; e, Laws, and pharynx opened along midventral line to show internal surface (arrow marks midpoint in length of pharynx); f, Ventral view of cuticle showing the small posterior sucker; g, Anterior region, male median region, and female reproductive system.

Somites and somital ganglia indicated by Roman figures, annuli, 'a', etc.; somital ganglia shown at relative size. Abbreviations: at., atrium; c.od., common oviduct; ce., vaginal caecum; ej.b., ejaculatory bulb; ej.d., ejaculatory duct; epid., epididymus; ov., ovary; pes., penis sheath; pr., prostate; va., vagina; va.d., vaginal duct.

All scales in millimetres. All drawings from the holotype.

narrow, wider inner and narrower outer dark bands. The margins light and continuous with the immaculate venter.

The anterior end obtusely rounded, narrow, the preclitellar region widening rapidly to the clitellum, slightly narrower behind this along the postclitellar region with parallel sides to the postnephric region which narrows abruptly to the base of the unusually small cupped sucker with the diameter about  $\frac{1}{3}$ rd of the maximum width of the body.

The male pore opens at the end of a low truncate cone formed by the margin of the genital aperture.

Total length, 38.0 mm; width at iv/v, 2.75 mm, at vii/viii, 4.0 mm, and the depth 2.0 mm increasing to 3.0 mm along the nephric region; width at x/xi, 8.0 mm and of this width along the clitellum and then briefly narrower to xxiv/xxv, rounding to form the base to the sucker, 2.0 mm, and the diameter of the sucker about 3.0 mm.

#### Colour

Preserved in alcohol: generally pale bluish grey with yellowish longitudinal stripes, the margin paler and continuous with the pale yellowish venter. Dorsum of the posterior sucker with a median dark patch, the sucker elsewhere of the colour of the venter.

The specimen has been long preserved. There is no indication of brownish or greenish tones, and the colour in life may possibly be blackish above, the light stripes, margins and venter all yellow.

#### Pattern Fig. 1 a-b

Preserved, faded. There is no indication of an ocular band, the ocular arch and margin of the velum are continuous with the margins. The somital sense organs are rarely detectable, nowhere as a series, and the topography of the pattern can only be estimated as:

(1) A light stripe occupying the median field and the paramedian line of sense organs (confirmed in viii) continues from the edge of the velum to the posterior border of xxvii. In this stripe there are faint indications of an interrupted narrow median dark band of the

width or narrower than the light stripes on either side between x and xv, and almost continuous from xv to xxiv.

These represent a dark median band and an inner pair of light stripes.

(2) An inner pair of dark bands fill the paramedian fields, extend from v/vi back to xxvii, being much clouded with paler colour along the middle of the band and to such a degree that this band appears along most of its length as composed of an inner and an outer band with erratic opposing margins; but this is a single band as shown by the fusion posteriorly in xxvii.

These correspond to paired bands of the paramedian fields, and as usual increase in width along the body as the fields widen.

(3) An outer pair of narrow light stripes of uniform width, generally a little wider than the inner pair, extend along the line of the intermediate sense organs and briefly into the fields on either side from about the middle of xi to xxiv or xxv.

(4) An outer pair of narrow dark bands define the outer pair of light stripes between the above levels and are generally of the width of the adjacent light stripe. It is possible that these bands include the supramarginal sense organs and extend briefly into the supramarginal field, but this could not be confirmed.

(5) The marginal stripe, wider than the other dorsal stripes, extends across the supramarginal field and is continuous on to the submarginal field.

#### Annulation Fig. 1 a-b

Interannular and intersomital furrows well-defined, equivalent, and the somital limits not directly recognizable along most of the body. Somital sense organs, small, rarely detectable; no obvious sensillae. Nephropores generally large, open, obvious.

The velum contracted, the margin thick, low convex, obtusely rounded, carrying the 1st and 2nd pairs of eyes in ii and iii; the first furrow iv  $a_1$   $a_2/a_3$ , so that  $a_1$   $a_2$  with the 3rd pair of eyes is not defined anteriorly and is continuous with the velum and  $a_1$   $a_2/a_3$  extends across the

median and paramedian fields, not to the margin of the sucker and there is no well-formed dorsolateral lobe; v, 2-annulate above, the 4th eyes in  $a_1$   $a_2 < a_3$ ,  $a_1$   $a_2/a_3$  reaches to the marginal line, and below this uniannulate v forms the lateral and ventral margin of the sucker; vi, 3-annulate above,  $a_1 < a_2 < a_3$ , the 5th eyes in  $a_2$ , and vi 2-annulate below with  $a_1$   $a_2 > a_3$ ; vii, 3-annulate above and below,  $a_1 < a_2 < a_3$ ; vii  $a_3$  and viii  $a_1$ , subequal; viii, 4-annulate,  $a_1 > a_2 > b_5 = b_6$ , 1st nephropores on  $a_1$ ; ix to xxiv, 5-annulate (total 16); ix,  $b_1 = b_2 < a_2 > b_5 > b_6$ ; x,  $b_1 = b_2 < a_2 < b_5 < b_6$ , with  $b_5$  the 1st annulus of the clitellum; xi,  $b_1 = b_2 = a_2 < b_5 > b_6$ ; xii,  $b_1 = b_2 < a_2 > b_5 > b_6$ ; xiii to xxii, the relative lengths of the annuli cannot always be determined with confidence on the dorsum, but these appear to be  $b_1 = b_2 < a_2 = b_5 = b_6$  in the midnephric group; xxiii and xxiv,  $b_1 = b_2 > a_2$  slightly  $> b_5 = b_6$ , the last nephropore on xxiv  $b_2$ ; xxv, 4-annulate,  $b_1 = b_2 = a_2 < a_3$ , and xxv  $a_3$  reduced but complete across the venter; xxvi, 2-annulate, somital organs posterior in  $a_1$   $a_2 > a_3$ ; xxvi/xxvii, incomplete across the median field; xxvii, uniannulate; the anus at the posterior border of xxvii: dorsum of the posterior sucker showing three concentric furrows, and one pair of paramedians.

#### *Alimentary tract Fig. 1 c-e*

Jaws small, compressed, the dorsomedian as high (0.35 mm) as wide at the base, narrowing to be subacute at the dental margin, housed in open recesses or grooves with such poorly defined margins as to be non-morphological; the dental margin very low convex, almost straight, 0.60 mm long; 39 teeth, strong, a gradually diminishing row, the teeth at the medial end, 20 microns high.

Salivary gland papillae present as a row of spaced small papillae parallel to the dental margin, and a few papillae scattered over the surfaces of the jaws.

The mouth and lumen of the pharynx slightly wider than usual, the mouth being distinctly wider than the base of the dorsomedian jaw; the lumen not obviously tapering; the wall of the pharynx, thin, smooth internally

with no indications of grooves dividing off muscular ridges (refer to the other material). Salivary glands diffuse, simple glands, ducts of the dorsal group aggregated into poorly defined columns of ducts. Radial muscles, an obvious sparse system.

The crop is swollen with consolidated blood. It is fragile and hinders dissection in the post-clitellar region.

The pharynx, short, terminating in the anterior annuli of ix at  $b_2/a_2$  with a short caecate compartment as the first portion of the crop in ix; x, a short compartment with a pair of minute caeca in the median position; xi to xiii, the compartments reduced by the heavily developed glandular layer of the clitellum, and almost tubular; xiv, a well formed compartment with obvious small paired caeca in the anterior position and larger paired caeca in the median position which extend into the paramedian chamber, as also in xv to xviii with the median caeca extending posteriorly to be lateral to the anterior caeca of the following somite; xix, with small anterior caeca and the caeca at the median level extending as postcaeca at least to xxv/xxvi; the compartment in xix is broad behind the origin of the postcaeca, connects terminally to the intestine which is tubular, inflated. The dissection was not continued to the rectum.

#### *Reproductive system Fig. 1g*

The indications are that the specimen is fully female mature with enlarged thin-walled ovaries, the vagina mucus-filled and swollen, and a heavy development of clitellar glands.

The genital pores are at xi  $b_5/b_6$  and xii  $b_5/b_6$ . The male aperture terminal on a wide-based low fleshy truncate papilla.

The organs on the anterior region of the male paired duct are in a linear relationship; the median regions, bimyomeric, mesomorphic, the female median region with a caecate vagina and vaginal duct.

The 1st testes are at xiii/xiv (dissection was not taken beyond this owing to the fragility of the crop). The vasa deferentia could not be examined anteriorly owing to the development of the clitellar glands. The convoluted folded epididymis consists of a narrow posterior

portion and a more broadly tubular anterior portion in the paramedian chamber in the anterior half of xii; the anterior portion of the epididymis tapering into the muscular ejaculatory bulb which is elongate cylindroid and the left partly folded on itself; ejaculatory bulbs taper into delicate ejaculatory ducts which pass into the median chamber and join independently into the ventral aspect of the muscular atrium which is continuous with the muscular penis sheath formed on a posteriorly directed primary loop reflecting at xi/xii so that the penis sheath is short, sturdy, relatively wide, and the initial recurrent limb dorsal to the terminal procurrent limb.

The enlarged ovaries are in the contiguous halves of xii and xiii; a short oviduct passes from the medial aspect of the anterior end of each ovary, the two joining together but without an indication of an atrium distinct from the common oviduct. The female median region formed on a posteriorly directed primary loop reflecting at xiii/xiv; common oviduct occupying nearly the entire length of the recurrent limb, is unusually wide, of uniform width and appearance along its length, and extends along and is intimately associated with the dorsal aspect of the vaginal duct, departing this posterior to the level of junction of the common oviduct with the vagina, and then briefly anteriorly to enter the vagina subterminally; the vaginal caecum, broad, shorter than wide; the vagina thin-walled, swollen, fusiform, terminating abruptly in the vaginal duct which is strongly muscular, continues directly to the genital pore without folds or convolutions, and occupies the procurrent loop.

The indications are that the vagina forms across the elbow of the primary loop, the common oviduct and vaginal duct occupying almost the entire length of the recurrent and procurrent limbs of the loop.

#### *Other material*

One specimen, Australian Museum, Sydney, G 11217, Lord Howe Island. Collector, Saunders, 1908.

Total length, 25.0 mm. Clitellum not evident, otherwise depressed and form as in the type with the margins parallel from xii to xxiv;

posterior sucker distinctly small, the diameter 2.5 mm and less than half the maximum width (6.0 mm) of the body.

Preserved, completely decolourized without any indication of eyes or pattern. Somital sense organs, not detectable; nephropores, minute.

General annulation as in type on the pre-nephric and post-nephric somites; annulation of the mid-nephric somites,  $b_1 = b_2$  slightly  $< a_2 = b_3$ , slightly  $> b_6$ , but while with the differences can be determined by measurement, they are so small that  $a_2$  is not recognizable with confidence by length alone, i.e. the annuli are essentially equivalent in length; xxvi/xxvii, incomplete across the median field.

Alimentary tract: Jaws, as in the type; papillae, very minute; internal surface of the pharynx with distinct dorsolateral grooves defining a dorsomedian ridge and the dorsal margins of the ventrolateral ridges, but these ridges are not further subdivided. The crop unsuitable for further detail.

Reproductive system, approaching male maturity. Regional and general morphology as in the type. Ejaculatory bulbs distinctly elongate cylindroid, each closely folded lengthwise into subequal limbs; male median region cylindrical, sturdy, reflected as a short loop in the contiguous halves of xi and xii. Oviducts, very short; no obvious atrial chamber and the atrium smoothly continuous with the wide oviduct; vagina, transverse, the caecum narrower than the body of the vagina, small and the length about twice the width; vaginal duct, heavily muscular, straight.

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